NITROGEN ECONOMY IN ARID AND SEMI-ARID PLANT COMMUNITIES.

Part III. The Symbiotic Nitrogen-fixing Organisms.

By N. C. W. Beadle, Department of Botany, University of New England, Armidale, N.S.W.

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Synopsis.

Of the 80 legumes investigated from the arid and semi-arid areas of eastern Australia, at least 68 produce effective rhizobial nodules (Mimosaceae and Papilionaceae); Caesalpiniaceae do not nodulate. Herbaceous species usually nodulate freely and many of them fix highly significant amounts of nitrogen. Some species of *Acacia* nodulate sporadically and tardily in the seedling condition and this is probably of significance with regard to regeneration, especially on eroded soils. Five species of *Rhizobium* occur and these are distributed discontinuously. Most soils contain at least one species of *Rhizobium*. Rhizobial populations are likely to be reduced or removed by soil movement under the action of wind.

Introduction.

In a previous publication (Beadle and Tchan, 1955) the widespread death of *Acacia aneura* (mulga), particularly in western New South Wales, and the consequent depletion of the sandy soils of their organic matter by the winnowing action of the wind were discussed as an introduction to the nitrogen economy of arid and semi-arid soils. Tchan and Beadle (1955) assessed quantitatively the possible accessions of soil nitrogen by non-symbiotic organisms.

The present paper deals qualitatively with the native legume-rhizobia systems, the data including nodulation records chiefly from field observations, the approximate distribution of the rhizobia of certain of the common native legumes, and an assessment of the significance of the various species as nitrogen-fixers in the plant communities in which they occur. Data on the introduced legumes (chiefly Trifolieae) will be presented in another paper.

The area covered in the field survey lies west of the 15-inch isohyet in western New South Wales and Queensland, between the Murray River and the highway linking Charleville and Windorah; isolated records come also from the Lake Eyre and Lake Amadeus Basins, and the Alice Springs and Oodnadatta districts. The plant communities in the main area of study are mentioned in Table 1; they have been described by Beadle (1948).

Relatively little work has been done on the inland legumes; some data on a few of the species, or on other species of common inland genera found in more humid regions, have been investigated with regard to nodulation (listed by Bowen, 1956, and unpublished data of Allen and Allen in personal communications).

Nodulation.

The roots of about 80 legume species have been examined in the field for the occurrence of nodules and 68 of these are reported on (Table 1). The remaining twelve, on which a definite statement cannot yet be made, may nodulate. Included in these twelve and of particular significance with regard to nitrogen economy (because they are community-dominants or abundant species) are *Acacia pendula* A. Cunn. (Myall), *A. harpophylla* F. Muell. (Brigalow), *A. cambagei* R. T. Baker (Gidgee), *A. loderi* Maiden, and *A. excelsa* Benth. (Ironwood); on all of these five species what appear to be nodule-scars have been recorded. The remaining inland species, including those which have been examined and those not, are rare in the field so that, even if they nodulate abundantly, their contribution to the fixed nitrogen in their respective communities must be small.

The data in Table 1 lead to the two generalizations: Firstly, with the exception of *Trigonella*, no genus is confined by a limited set of habitat conditions; this has some bearing on the distribution of specific rhizobia, which is discussed below. Secondly, members of the Papilionaceae and Mimosaceae nodulate in the field (with a very few exceptions), whereas Caesalpiniaceae do not.

Additional information from field observations, supplemented by pot tests made in the glasshouse, lead to the following comments and conclusions:

1. *Failure to record nodules.* This may be due to one or more of the following: (*a*) inability of the plant to nodulate; (*b*) absence of suitable rhizobia; (*c*) dry conditions at the time of digging when the nodules become desiccated and fragment, or the breaking off of nodules during sampling, especially in soils which form hard clods. By growing plants from seed in soil collected from around the roots of the same species (referred to as "own soil"), additional information was collected which provided the explanation for the absence of nodules from certain species. For example, *Cassia artemisioides* plants failed to produce nodules when supplied with cultured *Cassia* rhizobia, which suggests inability to nodulate; *Acacia oswaldii* and *A. colletioides* failed to produce nodules when grown in their own soil (from the mallee) but nodulated when supplied with *Acacia* rhizobia from crushed nodules from *A. rubida*, which implies an absence of rhizobia from the soil; *Glycyrrhiza anthocarpa* plants grown in their own soil to the 14-leaf stage produced only one nodule per plant, which probably indicates low numbers of the appropriate rhizobium in the field. Such observations are recorded in Table 1, column 5; a more detailed discussion of some of these points is given below.

2. *Nodulation and soil moisture.* Nodules are formed after rain and the life of the nodule is determined by the duration of moisture in the soil. Probably nodules rarely reach their maximum potential size, even in the case of annuals; this is suggested by the sizes of nodules developed on plants grown in pots, which are invariably larger than those in the field for both annual and perennial species. The only possible exceptions are the short-lived annuals, notably *Trigonella suavissima.* After the soils have dried out and the nodules have fragmented, nodule-scars are sometimes discernible on the roots. Perennial nodules probably rarely occur.

Since moisture plays a significant part in the abundance of nodules, the number of nodules per unit length of root usually increases (*a*) from arid to semi-arid (or wetter) for those species which have a wide climatic range and (*b*) in the same stand of a single species which spreads over a varying microtopography. The second condition is exemplified by *Psoralea eriantha* and *Swainsona burkittii*, both of which occur on sand dunes; on the crests of dunes nodules are rare and small (1–2 mm.) and white in colour (ineffectiveness is assumed), whereas at the bases of the dunes or in depressions where water lodges, nodules are larger and apparently effective. Plants of *Psoralea eriantha* grown in their own soil (sand from dune crests) in pots produced large effective nodules suggesting that inadequate moisture supply in the field is responsible for the small size of the nodules.

3. *Position of nodules on the roots.* From field and glasshouse data, nodules for both annuals and perennials may develop on either the taproot or lateral roots. In the field, the clustering of nodules at the top of the taproot has been observed in some species, notably species of *Psoralea*, and *Lotus coccineus*; the phenomenon is possibly due to the moister condition of the upper soil layers as a result of light showers of rain which fall after the plants have become established as seedlings or recommenced growth. Such nodules are often on short laterals.

4. *Depth of nodules in soil.* The location of nodules is determined partly by the distribution of the root system and partly by the rate at which the soils dry out. In the case of woody perennials, nodules rarely occur in the surface 10 cm.; they have been recorded in the case of *Acacia aneura* at a depth of 100 cm. In sandy soils (for annuals or perennials) nodules are rare in the surface 10 cm. of soil; in soils of heavy

TABLE 1.

Nodulation Records for Arid and Semi-Arid Legumes.

Explanation of terms, etc.: *Column 3*, Habitat: The terms "*mallee*", "*scrub*", "*woodland*" refer to the *Eucalyptus* mallee, *Acacia aneura* scrubs (often with associated species) and the *Eucalyptus* shrub woodlands respectively. "*Arid*" and "*semi-arid*" refer respectively to areas which receive less than 10 inches of rain per annum, and between 10 and about 15 inches. "*North*" refers to areas which receive a predominantly summer rainfall; "*south*" to areas receiving a predominantly winter rainfall. "*Watercourse*" includes all depressions (large or small) in which water flows after rains. *Column 4*, Abundance of nodules: "*Abundant*" is used to indicate two or more nodules per 10 cm. of root; "*common*" one nodule per 10 cm. of root; "*rare*" less than one nodule per 10 cm. of root. *Ineffectiveness* is assumed for nodules which were white and small (1–2 mm.). *Column 5*, Estimated significance: The estimate is subjective and is based on the abundance of the plant in the field, the number of nodules on the roots and their assumed effectiveness, and the nature of the leaves with respect to size, degree of xeromorphy and the number of leaves which fall to the ground annually.

1.	2.	3.	4.	5.
—	Habit of Plant.	Habitats in Arid and Semi-Arid Zones. Abundance in the Field. Soils.	Abundance of Nodules in the Field, their Shape and Size.	Estimated Significance of the Legume in Nitrogen Fixation in Communities in which it Occurs. Additional Comments.
		PAPILIONACEAE.		
Tribe PODALIREAE.				
Eutaxia microphylla (R.Br.) J. M. Black.	Perennial shrub to 40 cm. high, sometimes almost prostrate.	Mallee. Arid and semi-arid; south. Rare. Sandy soils.	Rare. Cylindrical, 6–8 mm. long.	Insignificant. Nodules may possibly be perennial in semi-arid areas.
Tribe HEDYSAREAE.				
Aeschynomene indica L.	Annual herb to 1 m. high.	Watercourses. Mainly semi-arid, north. Locally common. Clays.	Rare. Depressed globular, 5 mm. diam. Doubtfully effective.	Insignificant.
Desmodium varians Endl.	Weak herbaceous twiner, possibly perennial.	Chiefly woodlands. Semi-arid; north and south. Widely distributed but never common. Sandy loams to clays.	Abundant to rare. More or less globular, 4–5 mm. diam.	Probably significant.
Rhynchosia minima (L.) DC.	Trailing perennial.	Mostly watercourses; also mulga scrub. Arid and semi-arid; mainly north. Uncommon. Usually sandy soils.	Rare. More or less globular, 1–2 mm. diam.; possibly sometimes ineffective.	Insignificant.
Tribe LOTEAE.				
Lotus coccineus Schlecht.	Decumbent perennial herb, often forming mats.	Widely distributed in many communities, often abundant on plains. Arid and semi-arid; north and south. Sands to clays.	Usually abundant. More or less globular, 2–4 mm. diam.	Significant.
Tribe TRIFOLIEAE.				
Trigonella suavissima Lindl.	Decumbent or prostrate herb.	Mostly areas subject to flooding. Arid and semi-arid; north and south. Sometimes abundant. Usually clays.	Abundant to rare. Usually cylindrical, to 4 mm. long, sometimes coralloid, to 1 cm. across.	Significant.
Tribe GENISTEAE.				
Crotalaria cunninghamii R.Br.	Shrub to about 2 m. high.	Usually on loose sands. Arid; north. Locally common. Sands.	Rare. Cylindrical to globular, 2–3 mm. diam.	Insignificant.
C. dissitiflora Benth.	Shrub to 1½ m. high.	Scrubs on stable dunes. Arid; north. Locally common. Sandy soils.	Rare. Cylindrical, 5 mm. × 2 mm.; or 1 mm. and white (ineffective ?).	Insignificant.

TABLE 1.—*Continued.*

1. —	2. Habit of Plant.	3. Habitats in Arid and Semi-Arid Zones. Abundance in the Field. Soils.	4. Abundance of Nodules in the Field, their Shape and Size.	5. Estimated Significance of the Legume in Nitrogen Fixation in Communities in which it Occurs. Additional Comments.
		PAPILIONACEAE.—*Continued.*		
Templetonia egena (F. Muell.) Benth.	Leafless shrub to 2 m. high.	Mainly mallee. Arid and semi-arid; south. Rare. Usually sandy soils.	—	Plants grown in pots in own soils to 30-leaf stage produced no nodules.
Tribe GALEGEAE.				
Clianthus formosus (G.Don.) Ford et Vickery.	Prostrate annual herb, forming mats.	Rocky ridges, sandhills, scrubs. Arid; north and south. Sometimes locally common. Sands; skeletal soils.	Rare. Flat, cylindrical, sometimes notched at apex, 6–7 mm. long.	Doubtfully significant.
Glycyrrhiza anthocarpa (Lindl.) J. M. Black.	Shrub to 50 cm. high.	Areas subject to flooding. Arid; mainly north. Rare. Clays.	—	Cylindrical to semi-coralloid nodules to 7 mm. long developed on plants grown in own soil in pots.
Indigofera australis Willd.	Erect shrub to 1 m. high.	Mainly rocky outcrops. Mainly semi-arid; mainly north. Sometimes locally common. Sandy and skeletal soils.	Rare to common. More or less globular, to 4 mm. diam.	Possibly locally significant.
I. enneaphylla L.	Procumbent herb, possibly perennial.	Sandhills. Arid; north. Rare. Sands.	Rare. Cylindrical, 6 × 2–3 mm.	Insignificant.
I. hirsuta L.	Decumbent annual herb to 60 cm. high.	Scrubs and woodlands. Arid and semi-arid; north. Rare. Sandy soils.	Rare. Globular, to 3 mm. diam.	Insignificant.
I. linifolia Retz.	Prostrate herb, possibly perennial.	Sandhills, scrubs, woodlands. Arid and semi-arid. Rare to locally common. Sandy soils.	Rare. Globular, to 3 mm. diam.	Insignificant.
I. viscosa L.	Erect herb to 50 cm. high, possibly perennial.	Sandhills, scrubs, woodlands. Arid and semi-arid; north. Rare. Sandy soils.	Rare. Globular, to 3 mm. diam.	Probably insignificant.
Psoralea eriantha Benth.	Decumbent or semi-erect herb, usually perennial.	Usually on loose dunes. Arid; north. Locally common. Sands.	Rare. Usually 1–2 mm. diam., white, probably ineffective.	Insignificant. Plants grown in pots with rhizobia from *P. patens* produced large effective nodules.
P. patens Lindl.	Erect perennial shrub to 1 m. high.	Treeless areas, watercourses, less common in scrubs. Arid and semi-arid, chiefly north. Common. Sands to clays.	Common. Globular or irregular, up to 7 mm. across.	Significant.

TABLE 1.—*Continued.*

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		PAPILIONACEAE.—*Continued.*		
P. tenax Lindl.	Weak perennial herb to 40 cm. high.	Woodlands and treeless areas. Mainly semi-arid; mainly north. Common. Usually clays.	Common. Globular to irregular, up to 5 mm. across.	Significant.
Sesbania aculeata (Schreb.) Poir.	Shrub to 2 m. high, possibly perennial.	Watercourses, treeless areas. Arid and semi-arid; north. Rare to locally common. Clays.	Usually rare. Globular to irregular, to 5 mm. across; sometimes possibly ineffective.	Doubtfully significant in most areas. Abundantly nodulated plants recorded on Castlereagh River only.
Swainsona burkittii F. Muell. ex Benth.	Erect shrub to 80 cm. high, probably perennial.	Usually on loose sands, rarely in scrubs. Arid and semi-arid; south. Locally common. Sands.	Rare. Usually white, ½–1 mm. diam., except in table-drains, see next column.	Insignificant except in table-drains, where roots bear cylindrical nodules 4–5 × 2–3 mm.
S. campylantha F.Muell.	Straggling or erect herb to 60 cm. high; possibly perennial.	Many communities. Arid and semi-arid; mainly north. Rare. Chiefly heavy soils.	Rare. Globular, 1–2 mm. diam.	Insignificant.
S. fissimontana J. M. Black.	Decumbent or ascending herb with stems up to 40 cm. long, possibly perennial.	Rocky ridges. Arid. Barrier and neighbouring ranges. Locally common. Chiefly skeletal soils.	Common. Cylindrical, flat or coralloid, up to 7 mm. across.	Significant.
S. flavicarinata J. M. Black.	Prostrate herb forming mats. Behaves as an annual.	Saltbush plains east of Broken Hill only; extends westward and north. Rare. Clays.	Common. Flat, wedge-shaped, 6–7 mm. long.	Insignificant.
S. greyana Lindl.	Erect perennial to 1½ m. high.	Chiefly along rivers. Arid and semi-arid; north and south. Locally common. Chiefly clays.	Common to rare. More or less globular, to 3 mm. diam.	Significant.
S. lessertiifolia DC.	Weak erect herb, probably annual.	Scrubs. Mainly arid. Rare. Chiefly sands.	Rare. 1 mm. diam., white, possibly ineffective.	Insignificant. One record only.
S. microphylla A. Gray.	Prostrate or decumbent annual herb.	Many communities; widely distributed. Arid and semi-arid; north and south. Sometimes locally common. Chiefly sandy soils.	Rare, sometimes absent (arid areas). Cylindrical, 3–4 × 1 mm.	Perhaps locally significant in very good seasons.
S. oroboides F.Muell. ssp. *oroboides* Lee.	Weak erect or straggling herb, possibly perennial.	Widely distributed in many communities. Arid and semi-arid; mainly north. Locally common. Sandy soils to clays.	Common to rare. More or less globular, 2–3 mm. diam., sometimes smaller and white (ineffective ?).	Small to insignificant.
S. phacoides Benth. ssp. *phacoides* Lee.	Prostrate or ascending annual.	Many communities; often abundant on loose or stable dunes. Arid and semi-arid. Sandy soils.	Common to abundant. Flat, wedge-shaped or coralloid, up to 1 cm. across.	Significant.

TABLE 1.—*Continued.*

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		PAPILIONACEAE.—*Continued.*		
S. procumbens (F.Muell.) F.Muell. and *S. swainsonioides* (Benth.) Lee.	Ascending annuals forming dense mats.	Widely distributed, chiefly plains. Arid and semi-arid; north and south. Locally common; sometimes dominant. Chiefly heavy soils.	Abundant to rare. Globular, cylindrical or coralloid, up to 6 mm. across.	Highly significant. These two species are difficult to distinguish except when in flower. For comment on variability of nodulation, see text.
S. rigida (Benth.) J. M. Black.	Ascending annual herb.	Recorded only from sandhills along Darling River south of Menindee. Rare. Sands.	Common to rare. Cylindrical to wedge-shaped, 5–6 mm. long; or 1–2 mm. and white (ineffective ?).	Insignificant. Plants rare.
S. stipularis F.Muell.	Ascending annual herb.	Mainly plains; depressions in mulga scrub. Arid; mainly north. Sometimes locally common. Usually clays.	Common to rare. Cylindrical to globular, up to 5 mm. diam.	Significant. Plants appear only every few years but often in large numbers.
Tephrosia bidwillii Benth.	Decumbent or prostrate annual, often forming mats, possibly perennial.	Sandhills, mulga scrub and shrub woodlands. Arid and semi-arid, mainly north. Uncommon. Sandy soils.	Rare. 1–2 mm. diam., white, probably ineffective.	Insignificant.
Tribe PHASEOLEAE.				
Glycine sericea (F.Muell.) Benth.	Twining herb, probably perennial.	Rodky ridges, sand dunes, scrubs. Mainly arid; north and south. Rare. Sandy and skeletal soils.	Rare. 1 mm. diam., white, probably ineffective.	Insignificant. One record only of a larger nodule (5 mm. long).
G. tomentosa Benth.	Straggling perennial herb.	Mainly watercourses. Arid and semi-arid; north. Rare to locally common. Sands to clays.	Rare. 1 mm. diam., white, probably ineffective.	Insignificant.
Vigna lanceolata Benth.	Trailing herb.	Mainly watercourses. Arid and semi-arid; north. Rare to locally common. Sands to clays.	Rare. Ellipsoid, to 7 mm. long.	Probably insignificant.
		MIMOSACEAE.		
Tribe ACACIEAE.				
Acacia aneura F.Muell.	Usually shrub 4–5 m. high; sometimes a small tree.	Dominant over large areas of stable dunes and rocky outcrops; occurs also in woodlands. Arid and semi-arid; mainly north. Usually sandy soils.	Rare to common. Globular to cylindrical, up to 4 mm. diam.	Significant. Nodules developed on potted plants become coralloid and up to 15 mm. across.
A. buxifolia A.Cunn.	Shrub to 3 m. high.	Rocky outcrops, woodlands. Semi-arid; central N.S.W. Locally common. Skeletal and sandy soils,	Common. Globular, flat or coralloid, up to 7 mm. across,	Significant.

TABLE 1.—*Continued.*

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		MIMOSACEAE.—*Continued.*		
A. bynoeana Benth.	Shrub to 2 m. high.	Mallee. Arid; south. Rare. Sandy soils.	Common. Globular or cylindrical up to 5 mm. long.	Significant over very small areas.
A. cana Maiden.	Shrub to 3 m. high.	Locally dominant in parts of west Darling. Arid; north. Sandy soils to clays; sometimes saline.	Nodules scars recorded.	Possibly significant (data inadequate).
A. calamifolia Sweet.	Shrub to 3 m. high.	Woodlands, rocky ridges. Arid and semi-arid; north and south. Rare. Sandy and skeletal soils.	Rare to common. Globular. 2–3 mm. diam.	Insignificant. Abundant coralloid nodules developed on potted plants grown in own soil.
A. colletioides A.Cunn.	Shrub to 3 m. high.	Mallee, sandhills, rocky ridges. Arid and semi-arid; south. Uncommon. Sandy and skeletal soils.	——	Coralloid nodules have been developed on plants grown in own soil in pots, but only when rhizobia were added.
A. deanei (R. T. Baker) Welch, Coombs et McGlynn.	Shrub to 5 m. high.	Mainly woodlands. Semi-arid; south. Locally common. Sandy soils.	Common. Globular, up to 4 mm. diam.	Significant.
A. doratoxylon A.Cunn.	Shrub to 6 m. high, sometimes a small tree.	Rocky outcrops. Mainly semi-arid; north and south. Locally common. Skeletal soils.	Common. Globular, 2–3 mm. diam.	Probably significant.
A. estrophiolata F.Muell.	Tree to 15 m. high.	Stable dunes and rocky outcrops. Arid; north. Locally common. Sandy and skeletal soils.	——	Coralloid nodules developed on plants grown in pots.
A. farnesiana Willd.	Shrub to 5 m. high. Leaves bipinnate.	Watercourses, treeless areas. Arid and semi-arid; north; sometimes locally common or dominant. Clays.	Possibly common. Globular, up to 4 mm. diam.	Significant. Coralloid nodules developed on plants grown in pots.
A. gladiiformis A.Cunn.	Shrub to 3 m. high.	Rocky ridges, Barrier Range. Rare. Skeletal soils.	——	Insignificant. Abundant coralloid nodules on plants grown in pots.
A. hakeoides A.Cunn.	Shrub to 3 m. high.	Woodlands, mallee. Semi-arid; Central N.S.W. Locally common. Sandy soils.	Abundant. Globular, flat, cylindrical, coralloid, up to 1 cm. across.	Significant.
A. homalophylla A.Cunn.	Shrub to 6 m. high.	Woodlands, mallee. Mainly semi-arid; north and south. Often locally common or dominant. Sandy soils.	Usually common. Globular, cylindrical to coralloid, up to 8 mm. across.	Significant.
A. ligulata A.Cunn.	Shrub to 5 m. high.	Usually sandhills. Arid; north and south. Locally common or dominant. Sands.	Rare to common. Globular 2–3 mm. diam.	Significant.
A. oswaldii F.Muell.	Shrub to 4 m. high.	Many habitats; woodlands to treeless areas. Arid and semi-arid; north and south. Rare. Sands to clays.	——	Coralloid nodules developed on potted plants, but only when rhizobia were added.

TABLE 1.—*Continued.*

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		MIMOSACEAE.—*Continued.*		
A. rigens A.Cunn.	Shrubs to 2 m. high.	Mainly mallee. Arid and semi-arid; south. Locally common. Sandy soils.	Common. Cylindrical, up to 6 mm. long.	Significant, especially in semi-arid areas.
A. salicina Lindl.	Shrub, or small tree to 10 m. high.	In or near watercourses, rarely on dunes. Arid; north and south. Rare. Clays to sands.	Rare. Globular, 2–3 mm. diam.; or coralloid, 1 cm. across.	Insignificant.
A. stenophylla A.Cunn.	Tree to 15 m. high.	Watercourses. Arid, and semi-arid; north and south. Rare. Clays.	——	Nodules have not been developed on plants grown in their own soil in pots.
A. tetragonophylla F.Muell.	Shrub to 3 m. high.	Rocky ridges, dunes. Mainly arid; north. Sometimes common. Sands and skeletal soils.	Rare. Globular, 3 mm. diam.	Probably insignificant.
A. triptera Benth.	Shrub to 2 m. high.	Mallee. Semi-arid. Central N.S.W. Rare. Sands.	Rare. Globular, 2 mm. diam.	Insignificant.
A. victoriae Benth.	Shrub to 4 m. high.	Usually near watercourses. Arid; north and south. Often forms mono-specific communities in watercourses. Clays; skeletal and sandy soils.	Mostly rare. Cylindrical, bifurcating, coralloid, to 1 cm. across.	Probably significant.
Tribe ADENANTHEREAE. *Neptunia gracilis* Benth.	Procumbent shrub.	Overflow country, watercourses, woodlands, treeless areas. Mainly semi-arid; north. Sometimes common. Usually clays.	Common. Globular to irregular, up to 7 mm. across.	Significant.
N. monosperma F.Muell.	Procumbent shrub.	As *N. gracilis.*	Common. Globular to cylindrical, up to 5 mm. long.	Significant.
		CAESALPINIACEAE.		
Bauhinia carronnii F.Muell.	Tall shrub or small tree.	Bases of sand dunes. Arid; north. Usually rare, sometimes locally common. Sands.	Nodules not recorded.	Probably none.
Cassia artemisioides Gaudich., *C. desolata* F.Muell., *C. eremophila* A.Cunn., *C. phyllodinea* R.Br., *C. pleurocarpa* F.Muell., *C. sturtii* R.Br.	Shrubs to 3 m. high.	——	Nodules not recorded.	Probably none. No nodules recorded on plants of *C. artemisioides* or *C. eremophila* grown in own soil in pots. Cultured *Cassia* rhizobia failed to induce nodulation on potted plants.
Petalostylis labicheoides R.Br.	Shrub to 2 m. high.	Usually rocky outcrops, sometimes in scrubs. Arid; mainly north. Rare. Sands.	Nodules not recorded.	Probably none. No nodules developed on plants grown in own soil in pots.

texture, especially when subject to flooding (when they remain moist for periods of weeks), nodules on annuals and herbaceous perennials may occur as little as 1 cm. below the surface.

5. *Annual variation in abundance of nodules.* Those species which nodulate in the field produce nodules after rain at any time of the year, or during the appropriate season in the case of seasonal annuals. However, for certain species at least, the number of nodules produced from year to year or from season to season is by no means constant, but appears to vary with the interval between rains—the longer the interval the larger the number of nodules. The phenomenon was first observed in *Swainsona procumbens* which, during one good season following a dry spell of about three years at Fowler's Gap, north of Broken Hill, produced nodules at the rate of one per 2 cm. of root; one year later during a second good growing season for this species (which is an unusual occurrence) plants in the same area produced nodules at the rate of one per 50 cm. of root. A similar behaviour has been observed on two later occasions for this species in other parts of the State, and also for *Trigonella suavissima.* Likewise, similar variations in the nodulation pattern have been observed on marked plants of *Acacia aneura.* Suppression of nodulation of exotic herbaceous legumes through the accumulation of nitrate is a well-known phenomenon, and it is probable that the native legumes, both herbaceous and woody, are behaving in a similar fashion. This is of interest and of economic importance in so far as the suppression of nodulation must inevitably tend to limit the total nitrogen capital in the communities, especially the herbaceous ones. Unfortunately the problem is one that cannot be studied satisfactorily in the field since successive favourable years or seasons are the exception rather than the rule.

TABLE 2.

Time of Nodulation, Expressed in Terms of the Number of Leaves on the Seedling (excluding Cotyledons) when the First Nodule was Observed.

Species.	Number of Leaves.
Lotus coccineus	3
Psoralea eriantha	4
P. patens	3
Swainsona procumbens	4
Trigonella suavissima	Cotyledon stage
Acacia aneura	Usually 3 to 7
A. colletioides	About 25
A. estrophiolata	8
A. oswaldii	About 15
A. tetragonophylla	6
A. victoriae	4
A. rubida	3

6. *Age of plant and nodulation.* In Table 2 the ages of plants, expressed in terms of leaf number, at which the first nodules have been observed, are given. *Trigonella suavissima* is noteworthy because of its early infection. Dry land acacias, on the other hand, nodulate sporadically and tardily, and warrant further discussion.

It is probable that all species of *Acacia* are capable of nodulation if supplied with the appropriate rhizobia (Bowen, 1956). The difficulties in recording nodules on some of the inland species is due partly to lack of rhizobia in certain soils (discussed in the next section), partly to the generally dry conditions leading to infrequent nodulation, and partly also by what appears to be a paucity of suitable sites on the root for infection, which results in tardy or sporadic nodulation. This last condition has been recorded for four of the inland species that have been studied in pot culture (*A. aneura. A. colletioides, A. estrophiolata* and *A. oswaldii*). In contrast, *A. tetragonophylla* and *A. victoriae* nodulate fairly regularly at the stated stages (Table 2).

Tardy or sporadic nodulation means that the species in question (particularly *A. aneura*) are unreliable as test plants for the recovery of rhizobia from soils, and the use of *A. aneura* for this purpose had to be abandoned. As a substitute, *A. rubida*, a tableland species, was used in all tests, and in most cases both this species and *A. aneura* were sown in the same pot, thus enabling a comparison of the nodulation pattern of the two species to be made, with the following results: Firstly, when supplied with abundant rhizobia from crushed nodules, *A. rubida* nodulated at the three-leaf stage and nodules continued to form at the rate of two or three for each added leaf, up to the 12-leaf stage. *A. aneura*, on the other hand, grown in the same pot nodulated rarely at the 3-leaf stage but usually before the 7-leaf stage; the single nodule became very large (1–2 cm. across) and remained as the sole nodule on the plant up to the 12-leaf stage (in some cases a second or third much smaller nodule developed). Secondly, when the two species were grown together in soils from the *A. aneura* scrub, *A. rubida* nodulated as described above, but at the 12-leaf stage the number of nodules per plant was often fewer than 20, suggesting a lower rhizobial population in the soil than under the first condition. *Acacia aneura* rarely nodulated before the 7-leaf stage and rarely produced a second nodule before the 12-leaf stage. An examination of the root systems showed the following contrasting characters: *A. rubida* produced a much-branched root system, white in colour. The roots of *A. aneura* in contrast are branched but little, and are heavily pigmented with what are assumed to be tannin derivatives, so that they are brown. Seedlings of *A. aneura* at the 7-leaf stage usually had taproots 60 cm. long and a total root length of about 200 cm. (longest recorded 308 cm., with no nodules). These seedlings of *A. aneura*, grown in their own soil, were invariably stunted, with phyllodes 2–3 cm. long which frequently showed the yellowing indicative of N-deficiency. This yellowing disappeared in later-formed phyllodes, when nodulation had occurred. If these data are typical of *A. aneura* seedlings, they suggest that nodulation sites occur at the rate of one per 100 cm. of root. This figure, however, does not apply to mature plants in the field where nodules have been recovered from established plants at the rate of three or four per 10 cm. of root.

Geographic Distribution of Rhizobia.

Some observations on the distribution of the rhizobia of five genera have been made, sufficient to provide a general picture on the presence or absence in most plant communities. The data have been accumulated from field records supplemented by testing soils from 140 sites for rhizobia by the growing of seedlings. Most of the soils selected for investigation did not support nodulated legumes in the field (except assumed nodules on *Acacia aneura*); one or more species were grown in the soils (*A. rubida*, *Psoralea patens*, *Lotus coccineus* and *Trigonella suavissima*). Although controlled cross-inoculation tests were not carried out (except for *Psoralea*), there is every reason to believe, both from experiences of other workers (Norris, n.d.) and from the soil tests mentioned above, that cross-infection between the legumes tested does not occur, and consequently it is to be concluded that at least five specific populations of rhizobia are present in the arid and semi-arid regions.

Table 3 presents the data on distribution. The following points are of interest.

1. With the exception of the *Casuarina* scrubs and most of the arid mallee, all soils contain at least one species of *Rhizobium*. The absence of rhizobia from these two communities is perhaps not unexpected, since they contain extremely few legumes, through which rhizobial populations could be built up. Or perhaps the converse is true: the absence of rhizobia prevents or retards invasion by legumes. Furthermore, some of the mallee areas are extremely low in soil phosphate (about 15–20 p.p.m. HCl-soluble P), which factor may contribute towards the exclusion of both legumes and rhizobia.

2. Widespread throughout the entire area are the rhizobia of *Acacia*, *Lotus* and *Psoralea*. The rhizobia of *Acacia* and *Lotus* were recorded in soils collected from the

mulga scrub on stable dunes in the Lake Amadeus Basin, and that of *Psoralea* from heavy saline soils (abundantly nodulated plants) from the Lake Eyre Basin.

3. Within any community the populations of all species of rhizobia vary in space, presumably since populations are built up by societies of legumes. However, rhizobia of the herbaceous legumes have been recovered from soils which do not support the legume in the field; this may be an illusion, partly since crops of herbaceous legumes appear sporadically after the infrequent rains and partly since grazing by domestic stock has removed legumes over large areas or decreased their abundance. The distribution of the *Trigonella* rhizobium is especially perplexing: *Trigonella suavissima* occurs almost entirely on soils of heavy texture, chiefly along the major watercourses, around the inland lakes, and on some of the treeless plains, for example the Hay plains where it was first recorded by Mitchell (1838) at Lake Waljeers. Before the studies on the distribution of *Rhizobium meliloti* were made by Hely and Brockwell (1960), it was thought that *Trigonella* was infected only by the rhizobia from *Melilotus*. These two writers, however, show that *R. meliloti* from arid and semi-arid soils can infect and in some cases fix nitrogen in association with some species of *Medicago*. These findings must be viewed with caution with regard to the *Trigonella* rhizobium, since species of *Medicago* (chiefly *M. hispida*, *M. minima* and *M. laciniata*) now occur in

TABLE 3.

Approximate Distribution of the Rhizobia of Acacia, Psoralea, Lotus, Swainsona *and* Trigonella *according to Plant Community and/or Topography.*

+ indicates present, − probably absent, ± mostly present, ∓ mostly absent.

	Acacia.	*Psoralea.*	*Lotus.*	*Swainsona.*	*Trigonella.*
Moving dune-crests (arid)	−	±	−		−
Dry sandy creek beds (arid)	+	+	∓	∓	−
Acacia aneura scrubs on stable dunes	+	±	∓	∓	−
A. aneura scrubs on rocky ridges (tops)	+	−		∓	−
A. aneura scrubs on rocky ridges (bottoms and creeks)	+	+	∓	±	−
Mallee (arid)	∓	−	−	−	−
Mallee (semi-arid)	+	∓	−		−
Casuarina cristata scrubs (arid)	−	−	−		−
Atriplex vesicaria on stony downs	−	+	+	∓	∓
A. vesicaria on plains	−	+	+	+	±
Astrebla pectinata grassland	−	+	+		−
Eucalyptus populnea—Acacia shrub woodland	+	∓	∓	±	−
River flats (Darling R.)	±	+	±	±	±
River flats (semi-arid)	±	+	+	±	±

the west-Darling country both along and remote from the main rivers and, in the case of *M. hispida*, the plants are nodulated with rhizobia which will not infect *Trigonella* (tested by the present writer), which suggests that strains of *R. meliloti* are introduced with the *Medicago* and that the medics are not necessarily infected by the *Trigonella* rhizobia that originally existed. The presence of nodulated medics on sandy soils where *Trigonella* does not exist and has probably never existed supports this view. The finding of Vincent and Waters (unpublished data, quoted in Vincent, 1962) are relevant, namely, that isolates from *M. laciniata* will infect *Trigonella*, whereas isolates from other species of *Medicago* will not; this seems to explain the distribution of the *Trigonella* rhizobium provided by the present writer's observations from pot tests on 76 soil samples from the field. Of these samples, none are known to support *Trigonella* and about half were collected in the semi-arid zone where effectively nodulated medics are known to occur or are likely to occur. The *Trigonella* rhizobium was recovered from only five of these samples; one record, north of Tibooburra on the stony downs, can possibly be explained by the one-time presence of *Trigonella* in this area; the remaining four records from the Cobar and Bourke districts, on the grounds of Vincent and Waters' data, seem likely to be recoveries from *Medicago laciniata*, which species, abundantly and effectively nodulated, has been recorded by the writer in the Cobar district.

4. Rhizobia occur irrespective of soil texture. From the data available, populations of rhizobia are highest in sandy loams (except *Trigonella*). This is probably due to the abundance of legumes on such soils. This finding is in sharp contrast with the requirements of *R. trifolii* introduced into Western Australia where persistence of the rhizobia in sandy soils has proved difficult or impossible (Burvill, 1962; Parker, 1962). The ecological tolerances of the native rhizobia would thus appear to be different from those of *R. trifolii.* Furthermore, since different species of *Acacia*, *Psoralea* and *Swainsona* are in most cases confined to different kinds of soil, different strains of rhizobia may well exist.

5. *Psoralea patens* and *Lotus coccineus* occur on both saline and non-saline soils and nodulation may be abundant on both kinds of soil. A high salt tolerance of the rhizobia must be assumed from field evidence, a point which has been confirmed by Charley (unpublished data) in the laboratory, the rhizobia tolerating salt levels of 0·6 M. NaCl (in 2% agar), whereas germination of the seed and/or growth of seedlings of *Psoralea patens* were prevented by 0·2 to 0·3 M. NaCl.

Efficiency of the N–Fixing Mechanisms.

Some doubt has always existed as to whether the inland legumes are efficient nitrogen fixers, the doubt having arisen chiefly through the difficulty in recovering nodules in the field at any time when the legume happens to be dug. For reasons already discussed, absence of nodules at any one time does not imply that abundant fixation does not occur; conversely the presence of nodules on a plant cannot be used to indicate that the whole of the nitrogen in the plant has been derived from these nodules, since the plant may be absorbing free nitrate from the soil. It follows, therefore, that precise quantitative estimates of nitrogen fixation cannot be made merely by weighing and analysing crops of plants or leaves as they appear.

In order to test the efficiency of the nodules in fixing nitrogen and to compare growth by rhizobial fixation with that through absorption from nitrate solution, herbaceous plants and acacias were grown in the glasshouse, one set being fed with Hoagland's solution, the other with a nitrate-free solution based on Hoagland's solution and with the addition of specific rhizobia for each species. The herbaceous species used were *Swainsona fissimontana, Trigonella suavissima, Lotus coccineus, Psoralea patens, P. eriantha.* Nodulated plants in all cases grew as rapidly as the plants fed on Hoagland's solution and produced the same amount of dry matter. The tardy nodulation of the acacias rendered the comparison between nodulated and nitrate-fed plants useless. That fixation occurs, however, was apparent by the sudden increase in growth rate of seedlings, which coincided with the incidence of nodulation. Furthermore, analyses of leaves of ten effectively nodulated herbaceous species from the field gave N-contents (dry weight) ranging between 3·1% and 5·5%. The presumably ineffectively nodulated *Psoralea eriantha* had a N-content of 2·9%. Nodulated acacias from the field had a much higher N-content (about 2·0%) than *Hakea leucoptera* (0·5%), a sclerophyllous species growing with *A. aneura.*

These data suggest a significant N-fixing capacity in the field for those species which nodulate and a significant contribution to the N-capital of the community by those species which occur abundantly. The quantitative aspects will be dealt with in detail in a later publication.

Dispersal and Survival of Rhizobia.

Opportunities for dispersal of rhizobia are afforded by water movement along rivers and creeks and by the action of wind. Since the advent of white man and domestic stock in the inland, movement of soil by both water and wind has been greatly increased; exotic legumes and their rhizobia have been introduced, particularly in the wetter areas of eastern Australia, and from these areas and through the agency of the rivers which flow inland legumes, with or without their specific rhizobia, find appropriate migration paths to invade certain semi-arid and arid communities. Species of *Medicago* in particular and, locally, of *Vicia* and *Melilotus* have become naturalized in certain habitats, chiefly on clayey soils but also, in some areas, on soils of light texture. The plants are effectively nodulated and the presence of both legume and rhizobia can be accounted for either by migration along a watercourse or by slow movement from the more humid east to the west as far as the 10-inch isohyet. Isolated records of nodulated medics and of *Vicia* are abundant from the west-Darling remote from rivers and these can be accounted for by the chance transportation of seed (burr) and rhizobia by man or animals, possibly during the cooler periods of the year.

By analogy, the native rhizobia may follow or have followed similar migration paths. This, however, seems unlikely, since the migration of legumes and rhizobia, either native or exotic, from the clayey river-flats on to the adjacent sandy country does not occur in the arid zone, e.g., westward from the southern portion of the Darling River flats, though it is possible in the semi-arid zone. It appears that both the leguminous and rhizobial floras of the inland have developed quite independently of the eastern floras, having survived the extreme arid period through which the country passed before the present vegetation developed (Crocker, 1959). The restriction to the inland of several leguminous genera not endemic to Australia, such as *Glycyrrhiza*, *Isotropis*, *Clianthus* and *Trigonella* (the last with a specific rhizobium), favours this view.

Within communities, local migration of both legumes and their rhizobia under the influence of water have been observed for *Medicago hispida* and *Trigonella*, and in recent years migration paths have been created by roads, which have accelerated the spread of some herbaceous species, e.g., *Medicago* and *Psoralea*, in tabledrains where water often flows for long distances and where soils are invariably moister than the adjacent country.

It is improbable that winds play an important role in the migration of rhizobia in arid regions. The question must be left open until dust samples have been tested for the presence of living rhizobia. The action of wind in transporting soil, however, is likely to be destructive to rhizobia, as evidenced by tests made on soil samples collected from moving sand dune crests, moving soil surfaces, sandy accumulations along roadsides and fences, and recently colonized sandpatches (e.g., Broken Hill Regeneration Areas and the sandpatches at Fowler's Gap) which formerly were covered by mulga and which, today, have been stabilized by species of *Cassia*. Tests made on such samples showed that the *Acacia* rhizobium is usually lacking, while those of *Lotus*, *Swainsona* and *Psoralea* are sometimes present. The most tolerant to transportation by the wind appears to be *Psoralea*.

The absence of *Acacia* rhizobium in transported soils is significant with regard to the regeneration of *A. aneura*. Whereas regeneration of *A. aneura* in healthy stands of scrub is considerable, particularly in south-west Queensland and Central Australia, regeneration in the disturbed and degenerating scrubs, notably those in western New South Wales, is a rare occurrence. In addition to an ever decreasing seed supply and more extreme climatic conditions as a result of exposure of the soil surface and loss of organic matter, establishment of seedlings of *A. aneura* in these disturbed areas is made more difficult by the reduction in the rhizobial population, a factor which is accentuated by the tardy nodulation of this species. While a reduction in the rhizobial population may not be directly causal in the death of mature *A. aneura* plants, it is a factor which may contribute to the general weakening of the plant, and in this respect it is significant that rhizobia cannot always be recovered from soils below dead *A. aneura* plants, even though the soils have not been eroded by wind to a significant depth. The data available suggest the *Acacia* rhizobia live a far more precarious existence in the arid zone than do the rhizobia of the other plants that have been investigated.

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References.

BEADLE, N. C. W., 1948.—The vegetation and pastures of western New South Wales. Govt. Printer, Sydney.

BEADLE, N. C. W., and TCHAN, Y. T., 1955.—Nitrogen economy in semi-arid plant communities. Part I. The Environment and general considerations. PROC. LINN. SOC. N.S.W., 80: 62-70.

BOWEN, G. D., 1956.—Nodulation of legumes indigenous to Queensland. *Q. J. Agric. Sci.*, 13: 47-60.

BURVILL, G. H., 1962.—Light lands in Western Australia. 2. Their nature, distribution and climate. W. Aust. Dept. Agric. Bull. No. 3046.

CROCKER, R. L., 1959.—Past climatic fluctuations and their influence upon Australian vegetation. In "Biogeography and Ecology in Australia". Junk, den Haag, 283-289.

HELY, F. W., and BROCKWELL, J., 1960.—Ecology of medic root-nodule bacteria (*Rhizobium meliloti*) in arid zone soils. Proc. Arid Zone Tech. Conf., 1: 11/1-11/5.

MITCHELL, T. L., 1838.—Three expeditions into the interior of eastern Australia. London.

NORRIS, D. O. (n.d.).—Strain specificity, with particular reference to tropical legumes. C.S.I.R.O. Cunningham Laboratories. (Mimeograph.)

PARKER, C. A., 1962.—Light lands in Western Australia. 3. Microbiological problems in the establishment of legumes on light lands. W. Aust. Dept. Agric. Bull. No. 3046.

TCHAN, Y. T., and BEADLE, N. C. W., 1955.—Nitrogen economy in semi-arid plant communities. Part II. The non-symbiotic nitrogen-fixing organisms. PROC. LINN. SOC. N.S.W., 80: 97-104.

VINCENT, J. M., 1962.—Australian studies of the root-nodule bacteria. A Review. PROC. LINN. SOC. N.S.W., 87: 3-38.